ON THE FUNCTION OF THE OESOPHAGEAL DIVERTICULA IN THE ADULT FEMALE MOSQUITO

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(*Received for publication* 18 *February*, 1924)

The Oesophageal Diverticula are three sacs arising from the posterior portion of the oesophagus of the mosquito; they are present in both sexes. One sac, which is many times larger than the two others, lies ventrally in the thorax and the anterior portion of the abdomen, and opens on the ventral surface of the oesophagus at about the level of the first pair of legs; the distance to which it extends backwards in the abdomen varies according to the amount of food present in either the sac or the mid-gut; thus when the sac is full and the mid-gut empty, the former extends to the sixth or seventh segment, while when the mid-gut is full and the sac empty of food, the latter may be seen as a translucent area in the ventral portions of the first two abdominal segments. The two smaller sacs are dorso-lateral in position, lie in the thorax only, and open into the oesophagus at the same level as the large ventral sac. All three sacs contain a gas in the form of numerous bubbles; Hindle (1914) states that this gas is carbon dioxide produced by certain commensal fungi belonging to the *Entomophtoraceae*.

These organs have been described by a number of authors, the most complete and accurate account being that of Nuttall and Shipley (1903). These authors have also investigated the function of the sacs, and regard them as food-reservoirs. Their paper contains valuable discussions of the descriptions of several previous writers, and of various theories as to the function.

Christophers (1901) describes the organs briefly, and states that

' after feeding . . . . blood is very evident in the mid-gut and even in the calyx-like proventriculus, yet in the oesophagus there is no trace . . . . In a fed mosquito a transparent area is generally to be seen in front of the opaque mass of blood in the abdomen. This transparent area is the abdominal portion of the air-containing oesophageal diverticulum.'

Nuttall and Shipley (1903) describe experiments which they carried out to determine the function of the diverticula. These experiments, in which *Culex pipiens* was chiefly used, consisted in feeding the mosquitoes ' with blood-serum and sugar, either alone or together with carmine or neutral red. Sometimes the feedings took place alternately on coloured and uncoloured solution.' The results of these experiments are summarised in the following Table (Table I). Two experiments* (9 and 10) in which the number of insects used is not stated, are not included in the Table, but are given in Notes A and B below.

TABLE I.

Summary of Nuttall and Shipley's Experiments.

Mosquitoes fed on serum-sugar, either plain or coloured.

	Total	Food sacs	In gut	Remarks
Killed at once	3	3	1	A little in mid-gut of one
Killed after 1 hour	1	1	1	Most in ventral sac
Killed after 24 hours	5	5	2	Moderate amount in mid-gut. Note A.
Killed after 48 hours	5	5	1	Note B.
Fed again after 24 hours	6	6	6	Note C.
Fed again after 48 hours	2	2	2	Note D.

NOTE A. 'Experiment 9. Several insects fed on sugar-carmine-serum, killed after 24 hours showed carmine in intestine down to rectum, besides in ventral sac.'

NOTE B. 'Experiment 10. Several insects, treated as in 9, were killed after 48 hours, there being more carmine in intestine and rectum.'

* The numbers of the experiments refer to their order in Nuttall and Shipley's paper.

Note C. 'Experiment 14. Six insects, fed as in the preceding case (sugar-serum tinged with neutral-red) were fed again after 24 hours on clear sugar serum. The result was very striking. The contents of the ventral sac were coloured red, those of the stomach yellow, so that there could be no doubt but that the second meal had been almost entirely taken up by the stomach.'

Note D. In Experiments 4 and 5 the insects were fed as in 14, the interval being 48 hours. In one ' no bubbles in the much distended ventral sac, which contained carmine. Much aggregated carmine in the stomach.' In the other ' large bubbles and carmine in ventral sac. Little carmine in intestine, which contained some clear serum.'

Most writers subsequent to Nuttall and Shipley follow these authors in regarding the diverticula as food reservoirs. Thus, Patton and Cragg (1913) state that they ' are in fact, true food-reservoirs, as was first shown by Nuttall and Shipley. In mosquitoes killed during the act of feeding they are always found full of blood, while a little later, depending on the rate of digestion and, therefore, on the temperature, the blood is almost entirely confined to the mid-gut.' They point out, however, that the conditions of Nuttall and Shipley's experiments were highly artificial. Hindle (1914), also, regards the sacs as food reservoirs, but notes that the question is ' far from settled.'

In the course of some investigations on the Biology of the British Mosquitoes, the present writer found that although insects which had recently fed on blood were fairly common, he never encountered any which had the least trace of blood in the oesophageal diverticula. The species under investigation were *Anopheles maculipennis*, *Theobaldia annulata*, and *Culex pipiens*, and, at a later date, *A. bifurcatus* and *Aedes detritus*. He commenced experiments with *Anopheles maculipennis*, with the results shown in Table II ; these experiments, which had to be abandoned shortly after their commencement, consisted in feeding the insects on the human subject. At a later date he was able to resume the investigation ; this second series consisted of a repetition of his former work and also of Nuttall and Shipley's experiments using as food an aqueous solution of cane sugar tinged with neutral-red. This second series is summarised in Table III. In connection with the experiments with sugar solution as food, it was observed that the mosquitoes took a far longer time to gorge themselves than they usually take with a blood meal. In this second series of experiments the insects were killed by means

of ether immediately after feeding, and dissected at once. When the gut or sacs were not full of food they were carefully examined under a magnification of at least × 100.

Table II

Writer's First Series.

Mosquitoes fed on human subject.

	Total examined	Condition of Diverticula		
		Much blood	Trace of blood	No blood
Gorged, killed at once	14	1	3	10
Disturbed while feeding, killed immediately ...	11	0	3	8
Gorged, killed within 15 minutes	3	0	1	2
Gorged, killed within 60 minutes	2	0	1	1
Total	30	1	8	21

Table III.

Writer's Second Series.

Mosquitoes (*Anopheles maculipennis* and a few *Theobaldia annulata*) fed on human subject or on cane sugar—neutral red. All killed immediately after feeding.

	Total	Sacs		Gut	Remarks
		Much food	Trace of food		
Human subject ...	18	...	5	18	
Sugar—neutral red ...	23	23	...	...	
Fresh fruit juice ...	1	1	...	...	A *Theobaldia*, fed on a piece of orange

When we come to consider the various records, we find considerable discordance. Thus the statements of Christophers and of Patton and Cragg are entirely opposed to each other. The writer's own field observations and part of his experimental work favour Christophers' statements, while Nuttall and Shipley's results, and

those of the writer's experiments with 'artificial food,' strongly support the statements of Patton and Cragg.

It is generally agreed that the original food of the Culicidae was plant juices as it still is to-day in the case of the males of all species and the females of many, and that blood is an 'acquired taste.' If we consider the experimental evidence, we must agree that the experiments in which the food-material used most closely approximated to the primitive food of the insects were those of Nuttall and Shipley, and those of the present writer with sugar solution. In these the Oesophageal Diverticula were undoubtedly functional as food-reservoirs. In the case of blood-meals we are dealing with a more recently acquired character, and consequently must not be surprised to find, as we undoubtedly do, that the organs function irregularly.

In an experiment included in Table III, the writer found that fresh fruit juice was taken up into the ventral sac. In this connection it is interesting to note that Blacklock and Carter (1920) found that females of *Anopheles plumbeus* fed on human blood, 'when it was obvious that they had recently partaken freely of the raisin diet provided.' Presumably, the fruit juice was taken up by the diverticula and the blood by the gut.

The writer would suggest as a provisional hypothesis, that the original function of the Oesophageal Diverticula is that of food-reservoirs, but that this function is largely suspended in the case of blood-sucking females.

It has been suggested by some authors that these sacs, being 'air'-filled, would tend to buoy-up the insect when in flight. It is obvious that they would not function so, unless the density of the gases within was less than that of the external atmosphere, and, if Hindle is correct in his statement that the gas present is carbon dioxide, they would tend rather to weigh the insect down.

ACKNOWLEDGMENTS

The writer has much pleasure in taking this opportunity of thanking Professor R. Newstead, F.R.S., and Professor Warrington Yorke, M.D. for valuable suggestions as to the presentation of his results.

REFERENCES

Blacklock, B., and Carter, H. F. (1920). The Experimental Infection in England of *Anopheles plumbeus*, Stephens, and *Anopheles bifurcatus*, L., with *Plasmodium vivax*. *Ann. Trop. Med. and Parasit.*, Vol. XIII., pp. 413-420.

Christophers, S. R. (1901). The Anatomy and Histology of the Adult Female Mosquito. *Royal Society. Reports to Malaria Comm.*, Series 4, pp. 6-7. London.

Hindle, E. (1914). Flies in Relation to Disease ; Blood-sucking Flies. Cambridge. p. 58.

Nuttall, G. H. F., and Shipley, A. E. (1903). Studies in Relation to Malaria. II. The Structure and Biology of Anopheles (*Anopheles maculipennis*). The Digestive Organs. *Journ. Hyg.*, Vol. III, pp. 173-180.

Patton, W. S., and Cragg, F. W. (1913). A Textbook of Medical Entomology. Calcutta. pp. 110-111.